

COLONIALITY, MATE RETENTION, AND NEST-SITE CHARACTERISTICS IN THE SEMIPALMATED SANDPIPER

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ABSTRACT.—Coloniality is unusual among Scolopacidae. At Churchill, Manitoba, however, the small, remnant population of Semipalmated Sandpipers (*Calidris pusilla*) is highly clumped, with nesting density approximating 3–4 pairs/ha, and should be considered colonial. The species exhibits high fidelity to territory, mates, and nest sites—behaviors that promote rapid pair formation and allow experienced birds to increase their reproductive success by nesting earlier than pairs forming for the first time. The value of experience and early nesting was evidenced by the fact that six of seven returning young were produced by experienced pairs and had hatched on the first day of their respective nesting seasons. Nests were placed in dry locations very near open water. Those adjacent to small shrubs had slightly greater success, and young produced from these nests had much higher rates of return than those from nests placed amid sedges. In other parts of their breeding range, Semipalmated Sandpipers are also clumped and seem likely to be colonial. If so, estimates of breeding populations derived from indirect methods, such as habitat assessment from aerial photographs, will have limited applicability and will need to be complemented by ground-truthing. Received 3 October 2005, accepted 2 May 2006.

Spatial distribution in breeding birds runs the gamut from solitary nesting coupled with strongly developed territorial behavior to highly colonial, with the defended area being limited to the area that parents can protect without leaving their nests. Shorebirds (Charadrii) exhibit similar variation. Most are solitary nesters, but in some groups (e.g., Dromadidae, Recurvirostridae, Glareolinidae) coloniality is the rule, the extreme being attained by the Banded Stilt (*Cladorhynchus leucocephalus*), in which densities up to 18 nests/m² have been reported (Minton et al. 1995, del Hoyo et al. 1996, van Gils and Wiersma 1996). Lacking “objective (or even widely accepted) criteria as to how clumped nests must be to constitute a true colony,” ornithologists have used such terms as “semicolonial,” “strongly clumped,” or “loose colony” to describe situations in which “rather more dispersed nests . . . are . . . judged to be in a clump relative to the density of nests in the general vicinity” (Campbell and Lack 1985: 95). In any case, the essence of coloniality is that birds of a feather are disposed to nest near each other, the attraction being primarily social rather than to a common habitat.

Among Scolopacidae, coloniality of any kind is rare, and in the calidridine sandpipers (Calidridini) “semi-coloniality” has been reported or suspected only in the Western (*Cal-*

idris mauri) and Broad-billed (*Limicola falcinellus*) sandpipers (Palmer 1967, van Gils and Wiersma 1996). To this small list may be added the Semipalmated Sandpiper (*Calidris pusilla*), a monogamous and highly territorial species that breeds in the Subarctic and lower latitudes of the North American Arctic. Despite having been studied in only a few areas, its breeding biology is well-documented, mainly through comprehensive studies at La Pérouse Bay, Manitoba, by Gratto-Trevor (1992, and references therein). Although known to nest at relatively high densities, the Semipalmated Sandpiper has not been suspected of nesting colonially. At Churchill, Manitoba, however, that appears to be the case. Here I present observations on Semipalmated Sandpiper spacing and nesting behavior, along with information on nest-site characteristics, philopatry, and other aspects of the species’ breeding biology that complement and extend Gratto-Trevor’s findings.

METHODS

Observations were made in a potential nesting area of 7,000 ha in the “immediate Churchill Area” (Jehl and Lin 2001, map in Jehl 2004: 58° 45’ N, 94° 00’ W) from 1993 through 2004 as part of a broader study on shorebird biology (Jehl and Lin 2001, Jehl 2004). From previous studies in 1964 through 1967, I was familiar with the status of shorebirds in the Churchill area (Jehl and Smith 1970). When I resumed studies in 1991, I

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failed to encounter Semipalmated Sandpipers until 1993, when I found a few pairs nesting in a small meadow (~25 ha) 25 km east of the Churchill townsite. Then, and in each subsequent year, I attempted to find all nests and mark all individuals. I trapped adults at the nest in a simple walk-in trap and banded them with aluminum bands (or stainless steel, when available) and individually coded colored plastic bands. I made standard measurements with dial calipers (culmen and tarsus to 0.1 mm; flattened wing to 1 mm) and weighed each bird on a digital scale (to 0.1 g). Chicks were banded (but not color-marked) before they left the nest. From this effort, the identities of most adults (88% of 93 from 1993 to 2001) and young (73% of 120 from 1993 to 2000) were known, which allowed their status, mates, distribution, and nesting success to be followed from year to year. I aged adults on the basis of Gratto and Morrison's (1981) observation that most first-year birds are distinguishable from older birds by having up to four newly replaced outer primaries. Observations in 2001 through 2004 focused on documenting the identities of returned birds.

In most calidridines, males are typically smaller (e.g., Jehl and Murray 1985), but there is much overlap. To determine sex, I also used behavioral information, including observations that males defend territories much more strongly, sing longer and more complex songs, and are bolder around the nest. For birds returning in subsequent years, it was usually possible to use behavior to test earlier determinations: in only 2 of 25 cases did a tentative sexing need to be reconsidered.

RESULTS

Phenology and colony designation.—Semipalmated Sandpipers migrate through the Churchill region between the last days of May and the first third of June. Locally nesting birds move immediately to breeding areas, where they engage in prolonged and conspicuous territorial and courtship displays. Display flights take place at elevations of 40–50 m and may last 10 min or more. Typically, these displays involve several birds, which chase back and forth over, and well beyond, the nesting area.

From 1993 through 2004, the only Semipalmated Sandpipers nesting in the potential

(7,000 ha) nesting area occurred in the 25-ha meadow described above. Bordered by two lakes and dotted with shallow ponds that dried out by late June, the area was relatively wet and contained slightly more shrubby vegetation than some other nearby sites. Because (1) the nesting area occupied only 3–4 ha of this meadow, (2) nest density was extremely high (see below), (3) similar habitat elsewhere in the Churchill area was unused, (4) the historic distribution of Semipalmated Sandpipers at Churchill had not been limited to this type of habitat, and (5) nesting areas used through the 1960s, though largely unchanged, were no longer used, it was clear that the birds were attracted to each other and not to any specific habitat or topographic conditions. Consequently, their nesting behavior could be described as colonial. Elsewhere in the Churchill area, I encountered Semipalmated Sandpipers only twice from 1993 through 2004: one unpaired male, and an apparent pair, each located >5 km from the colony. All three birds disappeared after a few days.

The colony contained five pairs in 1993. Colony size had increased slightly by 1995 (11 nests; Table 1) and (probably) 1996, but runoff in 1996 flooded some early nests and may have prevented some pairs from finding suitable territories or re-nesting. In 1997, the number of adults was halved and I found only two nests. Subsequently, through 2001, the colony size fluctuated from two to three pairs, and by 2003 (and perhaps 2004) there was only a single, unpaired male. At maximum size in 1995 (Fig. 1), the colony encompassed 3.4 ha (determined by a polygon drawn around the outermost nests; this area included open-water areas where nesting was impossible), had a maximum linear extent of 416 m, and a density of 3.2 pairs/ha (maximum = 4.1 in 1993). Nests were tightly packed, the nearest-neighbor distance averaging about 55 m (minimum = 31 m).

Mate fidelity.—As in some other calidridines (e.g., Least Sandpiper, *Calidris minutilla*; Silt Sandpiper, *C. himantopus*; Dunlin, *C. alpina*; Jehl 1970; JRJ unpubl. data), Semipalmated Sandpipers form long-term bonds and pairs tend to re-occupy former territories as long as both members are alive (see also Gratto et al. 1985). In 16 cases in this study, both partners returned, pairs reunited 13 times in the follow-

TABLE 1. Population size and density of Semipalmated Sandpipers at Churchill, Manitoba, 1993–2001.

Year	Population size ^a	No. nests	Nesting area (ha) ^c	No. pairs/ha ^c	Maximum extent of colony (m)	Distance to nearest nest(s): [range] and median (m)
1993	≥10	5	1.2	4.1	126	[54–181] 87.3
1994	16–19	8	2.8	2.9	268	[52–63] 55.1
1995	22–24	11	3.4	3.2	416	[31–101] 54.4
1996	21–22	8 ^b	2.7	2.9	381	[37–124] 88.4
1997	12	2	—	—	121	121
1998	7	3	—	—	274	[84–193]
1999	4	2	—	—	—	55
2000	6–8	3	—	—	—	90, 91
2001	≥6	3	—	—	—	—

^a Estimated number of adults in colony early in the season.

^b Omits one renesting.

^c Could not be calculated from two points or when nests were arranged linearly.

ing season, and all had nested successfully in the previous year. Three pairs divorced (one previously successful, two unsuccessful). The successful male acquired a new mate and his old mate soon disappeared. Of the two previously unsuccessful pairs, the nest of one was flooded, the female acquired a new mate, and the old male skipped breeding; both birds of

the other pair acquired new partners, but the males retained their previous nest sites. Of the pairs that reunited, two remained intact for four seasons, three for three seasons, and two for two seasons.

Nineteen pairs failed to reunite. The reasons can only be guessed, as banded but unidentified birds occasionally showed up early in the

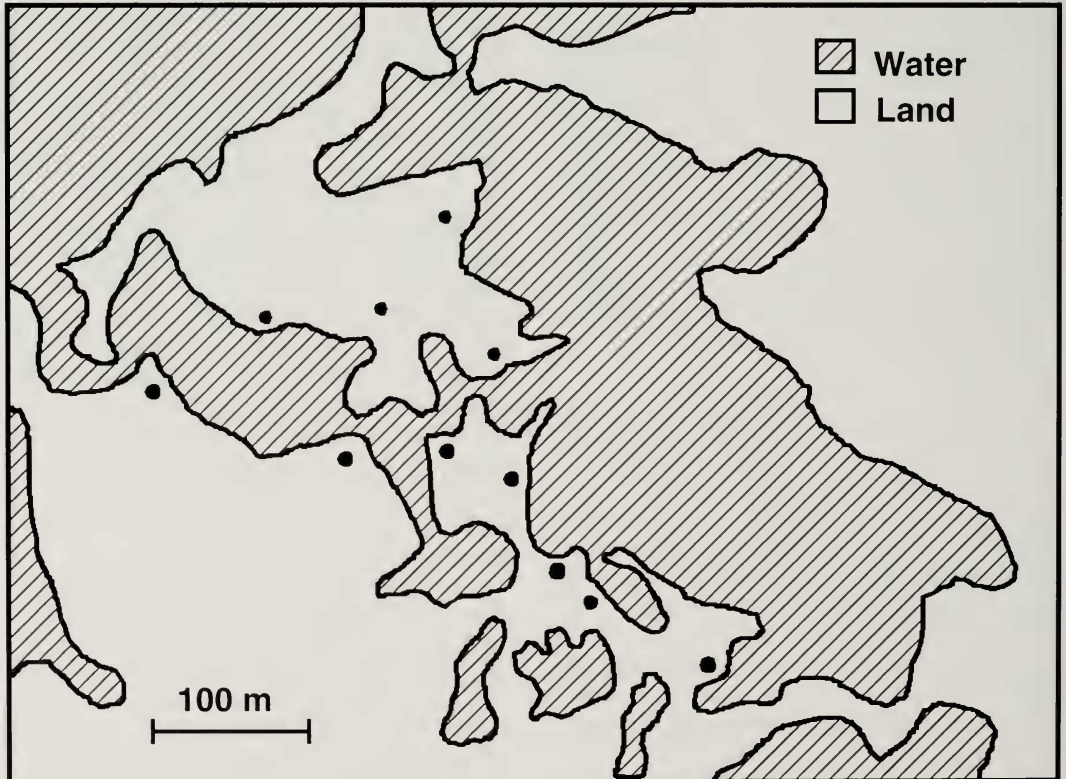


FIG. 1. Location and spacing of Semipalmated Sandpiper nests (●) at Churchill, Manitoba, 1995.

TABLE 2. Spacing and dispersal of Semipalmated Sandpipers at Churchill and La Pérouse Bay, Manitoba.

Variable	Churchill 1993–2001		La Pérouse Bay 1980–1984 ^a	
	<i>n</i>	Spacing, behavior	<i>n</i>	Spacing, behavior
Size of breeding area; habitat		3–4 ha; a single small meadow		2 km ² ; on delta of Mast River
Population size; density		2–11 pairs; 3–4/ha		100 pairs; 1/ha
Pairs reuniting, if both alive	16	13 (81%)	79	64 (81%)
Reuse of old nest cup	41	8 (19.5%)	305	13 (4.3%)
Rate of nest reuse if both parents returned	13	8 (61.5%)		No data
Nest shift: reunited pairs	14	Range = 0–85 m; mean = 25.4 ± 36 m; mode = 0 m	168	Range = 0–575 m; annual medians: 40–66 m
Nest shift: female mate change	8	4–360 m, mean = 153 ± 126 m; median = 115m	33	Range = 23–825 m; annual medians: 138–174 m

^a From Gratto et al. (1985).

year and then disappeared, perhaps without mating or perhaps because their nest was lost before I could find it. In several cases, the break-up was evidently due to bad timing (one partner returned late) or the unavailability of a previous nest site (see below).

Nest-site selection and site tenacity.—Just as Semipalmated Sandpipers tend to retain mates and territories from year to year, they also retain nest sites, as long as the previous nesting attempt was successful, the mate remains alive, and the nest is in suitable condition and does not contain unhatched eggs from the previous season. Of 13 cases in which both mates returned and reunited, the distance to subsequent nests ranged from 0 to 85 m (mode = 0 m; Table 2). One pair used the same nest for 4 successive years.

Semipalmated Sandpipers selected nest locations very near ponds (mean = 10.9 m ± 8.8, range = 0.5–29.5 m, *n* = 26), but placed their nests in dry situations on the sides or tops of small hummocks or ridges. Two types of nest sites were used: “shrub” sites were located under, or adjacent to, small bushes—in this case sweetgale (*Myrica gale*) or dwarf birch (*Betula nana*)—which typically allowed access from only one direction; “sedge” sites were in low, damp areas and nests were placed in a clump of sedge (*Carex* spp.). At 41 documented sites (including those reused by the same pair in subsequent years), 30 were in shrub and 11 in sedge. Nesting success was slightly (but not significantly) greater in shrub sites (83% versus 72%), which are better concealed and less subject to flooding. However,

the greater desirability of shrub sites was clear from their retention rates. Of 25 successful shrub sites, 14 (56%) were reused, 13 by a returning pair and 1 by a male with a new mate. Of the 11 successful shrub sites that were not reused, the nest cup or habitat had become unusable (*n* = 3) or one or both mates failed to return (*n* = 8). In sedge sites, 8 of 11 nestings were successful, yet none was reoccupied (1 site was used several years later by a pair with no previous breeding experience; the nest failed). In the other cases, the habitat had changed over the intervening winter (*n* = 3) or one or both mates failed to return (*n* = 4).

Among individuals that moved to a new location, males (*n* = 9) tended to stay near their previous nest site (median distance = 40 m). Eight paired with females that had no previous experience, and one bred successfully in the same territory for 4 successive years, each time with a new mate and each time moving ~50 m away from the previous site before returning to the original nest in the 4th year. Females (*n* = 8) tended to move farther away from previous nest sites (median = 115 m). Three females paired with experienced males that held territories near the center of the colony; one of these birds failed to nest one year when her nest was flooded, but she returned to her old territory (by then held by a different male) and nested within 4 m of the original scrape. The other five females bred with inexperienced males, whose nests in all but one case were on the periphery of the colony. One pair in its 2nd year moved 60 m, then 80 m

in year 3, and 80 m again in year 4. When the nest was flooded in year 4, the birds moved 85 m, which brought them to within 4 m of their original nest.

Of 120 local chicks banded, 7 returned to breed. At least six of these were produced by pairs in which at least one parent had nested successfully in a previous year; five (including two from the same clutch) were produced by two pairs. All returning young paired with inexperienced mates; the males ($n = 5$) moved 130–225 m (mean = 197 m) and the females ($n = 2$) moved 85 and 226 m from their natal sites. When the colony was relatively large, young males, with one exception, were only able to obtain territories at the colony edge. One bred on the periphery in his 1st year and then moved to a more central site in his 2nd year. Another male obtained a central location at first breeding, but only after experienced neighbors had reduced territory defense (cf. Jehl 1973) and started incubating; its young hatched a week later than those of other pairs.

DISCUSSION

Breeding behavior.—The aspects of mate and territory retention, philopatry, and dispersal treated in this study largely conform to those reported by Gratto et al. (1985) at La Pérouse Bay, ~30 km to the east (Table 2). At Churchill, nest density was greater than it was at La Pérouse Bay (3–4 versus 1 pair/ha), returning pairs dispersed much less (if at all) from previous nests, and reuse of the nest cup was greater (19.5% versus 4.3%; 61.5% [this study] if both pair members returned). These differences were probably related to topography and the size and stability of the respective nesting areas. Churchill birds were restricted to a small meadow, whereas Semipalmated Sandpipers at La Pérouse Bay bred on a river delta that often experienced high flows during runoff, resulting in greater loss of old nest cups. At Churchill, young males tended to breed at the colony's edge but did not disperse as far from their natal sites as they did at La Pérouse Bay (197 m versus 549 m, respectively), probably because the colony was much smaller.

For any species, the timing of breeding is critical to reproductive success (Lack 1968), and it is widely acknowledged that individuals nesting earlier—nearly always experienced

birds—typically have greater success than those that start later (e.g., Soikkeli 1967, Jehl 1970, Gratto et al. 1983, Black 1996, Handel and Gill 2000, Ruthrauff and McCaffery 2005). Early breeding is enhanced by high rates of territory, mate, and nest-site retention, which allow mates to begin nesting as soon as habitat conditions permit. These behaviors are especially important where breeding seasons are short, so it is not surprising that they have been reported in a variety of shorebirds that nest in the Arctic, including Dunlin, Least and Stilt sandpipers, and Black Turnstone (*Ar-enaria melanocephala*; Soikkeli 1967; Jehl 1970, 1973; Gratto et al. 1985; Jönsson 1987; Handel and Gill 2000; Sandercock et al. 2005; JRJ unpubl. data). In this study the importance of adult experience and early nesting was confirmed by the observation that six of the seven chicks that returned to nest were not only produced by experienced parents but also hatched on the 1st day of their respective hatching periods. The one exception hatched from the penultimate nest of its season and was produced by a pair that had not nested together previously. Although the female had no known experience, the male had bred successfully twice. Whereas the experience of both parents is surely relevant, that of the male is paramount because in this species and many other sandpipers, he takes the sole or major role in rearing the chicks from hatching to fledging (Jehl 1973, Gratto-Trevor 1991; JRJ unpubl. data).

Territory function and spacing.—When not incubating, Semipalmated Sandpipers left their territories and departed the colony area. Some moved to the mudflats of Hudson Bay, a minimum distance of 2–3 km, whereas when water levels were low inland, several might have fed together on mudflats in a lake bordering the colony. Because territory in this species is not based on food availability, it appears that nest spacing is determined by a balance between attraction to conspecifics and the need to maintain sufficient distance between neighbors to prevent predators from finding nests.

Density and population estimates.—Semipalmated Sandpipers are reported to nest at greater densities than other sandpipers, except perhaps the Western Sandpiper. On the North Slope of Alaska, where the Semipalmated

Sandpiper is abundant, Cotter and Andres (2000) reported mean densities of 30 pairs/km²; farther inland they noted up to 21.3 nests/km². At La Pérouse Bay, Manitoba, Gratto et al. (1985) estimated territory size to be 1.0 ha, including defended water areas (maximum density was 2.3 pairs/ha, based on dry land areas). At Churchill, density was even greater, reaching up to 4 pairs/ha (= 400 pairs/km², inclusive of pond areas). While all populations of Semipalmated Sandpipers do not necessarily have the same nesting habits (e.g., Gratto and Cooke 1987), spacing is also clumped in the three breeding localities closest to Churchill: Gordon Point and Fox Island (Jehl 2004; JRJ unpubl. data) and La Pérouse Bay (C. Gratto-Trevor pers. comm.). This and the high densities reported elsewhere suggest that the species is probably colonial throughout its range. If so, estimates of breeding populations derived from indirect methods, such as habitat assessment from satellite photography or vegetation maps (e.g., Gratto-Trevor 1996), will have limited applicability. Additional documentation of the kinds of breeding behavior reported in this paper, complemented by ground-truthing of nest spacing in different geographic regions, will be useful.

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